A HETEROPHYLLOUS CHEIROLEPIDIACEOUS CONIFER FROM THE CRETACEOUS OF EAST CHINA

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ABSTRACT. *Suturovagina intermedia* Chow and Tsao (Cheirolepidiaceae) from the Cretaceous of China is redescribed and emended on the basis of abundant new material. Its leafy shoots are heterophyllous and show axillary branching. The juvenile shoots bear widely spaced scale leaves, while mature ones bear mainly broad leaves enclosing most or the whole of the stem, with either a gap or a suture between the two lateral edges. Leaves of different types of shoot are generally similar in cuticular structures. Their stomata differ from all other members of this family in the very elongated subsidiary cells which form a tube- to truncated cone-shaped projection. Some dispersed fossil secondary xylem of *Protopodocarpoxylon*-type proves to belong to the same plant. An associated male cone, *Classostrobus cathayanus* sp. nov. yielding *Classopollis* pollen is also referred to it. This is the largest male cone so far known from this family.

THE present paper contains a revised description of *Suturovagina intermedia* Chow and Tsao 1977, based on the abundant material collected in 1979 from Zhouchiawen, Qiya Town, in the eastern outskirts of Nanjing (Nanking) City, Jiangsu (Kiangsu) Province, East China. The plant-bearing formation consists mainly of greyish calcareous siltstones and fine-grained sandstones. It forms well-exposed but discontinuous outcrops on the south bank of the Yangtze River near Nanjing. The original type specimens of *S. intermedia* were collected from this same formation, though at a different locality (Shenglicun, Yanziji), some 15 km away from Qiya Town. The geological age of the formation has not yet been settled. Some consider that it may be correlated with the Gecun Formation in Jurong County, east of Qiya Town, which is regarded on palynological evidence (Zhang 1962) as being of lower Cretaceous age. No other fossils, however, have hitherto been found in the plant-bearing formation, nor has any detailed palynological work been done, which could confirm such a correlation. The plant megafossils described in this paper clearly indicate a Cretaceous age for the formation.

MATERIAL AND METHODS

S. intermedia is almost the only species of plant megafossil to have been found in this plant-bearing formation. Besides some large hand specimens with branched shoots or cones, thousands of fragments were obtained by bulk maceration of several kilograms of rock. The material consists of fragments of leafy shoots, secondary xylem, and male cones. Some small doubtful fragments of female organs have also been found, but they will not be described until better-preserved specimens are available. All the specimens described here have been deposited in the Institute of Geology and Palaeontology, Academia Sinica, Nanjing, China.

After bulk maceration in either HCl or HNO$_3$, the picked specimens were washed in HF to remove adhering sand grains. They were then examined with a binocular microscope and photographed dry or under paraffin. Most of the hand specimens were photographed under paraffin. The conventional maceration method using Schulze's solution was adopted for both compressed leaves and male cones. The compressed and fusainized fragments of secondary xylem were cut with a scalpel to expose fresh surfaces. All prepared specimens were examined and photographed with a Leitz Dialux 20 light microscope with an attached camera, or with a Super II ISI scanning electron microscope.

DESCRIPTIONS AND COMPARISONS

*Leafy shoot*

Genus *Suturovagina* Chow and Tsao 1977

Type species. S. intermedia Chow and Tsao, 1977, p. 167.

Emended generic diagnosis. Plant with heterophyllous axillary branching shoots. Leaves persistent, adpressed, and spirally arranged; those on the juvenile shoot scale-like, and borne at intervals; those on the mature shoot, broad, scale-like, and imbricate, or more commonly slightly overlapping (occasionally separated), encircling most or all of the stem, leaving either a gap or a suture between the two lateral edges. Decurrent leaf base cushion crescentic, rhomboidal to short cylindrical with oblique ends. Stomata present on the abaxial cuticle, generally arranged in rows, actinocytic and monocyclic. Guard cells sunken at the bottom of a deep stomatal pit formed by vertical extension of the subsidiary cells. Subsidiary cells numerous.

Discussion. As implied by the specific name of the type species, *Suturovagina* is 'intermediate' in gross morphology of the leafy shoot between *Hirmeriella* (*Brachyphyllum* type) (Hörhammer 1933; Hirmer and Hörhammer 1934; Kendall 1947; Jung 1968; Harris 1979) and *Pseudofrenelopsis* (Nathorst 1893; Watson 1977). Both *Brachyphyllum*-type shoots with imbricate scale leaves and shoots with open-sheathed leaves, as in some *Pseudofrenelopsis*, are known to be present in *S. intermedia*. The *Brachyphyllum*-type shoot (text-figs. 1A, 2A, B, etc.), however, is not the prevailing one. It occurs probably only as the ultimate branchlet or the terminal portion of ultimate branchlets on the mature shoot. The shoot with open sheathed leaves (text-figs. 1B, C, E) is the predominant type in *Suturovagina*, while in *Pseudofrenelopsis* (Watson 1977; Alvin *et al.* 1978, p. 854) the shoot with close-sheathed leaves predominates. Though thousands of fragments have been examined, no typical shoot of *Pseudofrenelopsis* with close-sheathed leaves separated by long internodes was found. Only occasional shoots with complete-sheathed leaves in which the suture is very short and sometimes only represented by an inconspicuous notch, bear a resemblance to some of the shoots of *Pseudo-frenelopsis*, though the leaves in such shoots are very short, and the length of the decurrent leaf base cushion (internode) rarely exceeds the breadth of the stem (text-fig. 2I). The shoot with scale leaves at intervals (shoot type 1; text-figs. 1D, 2E, F, G, H) is not known in any species of *Hirmeriella* or *Pseudofrenelopsis*, nor is the shoot with open-sheathed leaves which do not overlap, but are more or less separated from each other (Pl. 75, fig. 6), even though these two genera are abundant in some localities (e.g. *Pseudofrenelopsis* in the Isle of Wight). Theoretically, shoot type 1 could be derived from an ordinary shoot with imbricate scale leaves, by a very rapid acropetal growth of the apical meristem so that the primordia of leaves emerge at rather long plastochrons. Nevertheless, it appears to be a new type of leafy shoot for the Cheirolepidiaceae (Hirmerellaceae) as well as for the Coniferales.

The stomatal structure of *Suturovagina* (text-fig. 1G) is characteristic, and readily distinguishable from *Hirmeriella* (*Brachyphyllum*) and *Pseudofrenelopsis*. Nor do I know of any other conifer genus, living or fossil, with a similar stomatal structure. The great extension of the subsidiary cells is unique, though in many conifers hairs or papillae are not uncommonly seen on the periclinal walls of subsidiary cells.

Heterophylly has been reported in most genera of Cheirolepidiaceae. Some types of leafy shoots are, moreover, not restricted to any particular genus. The *Brachyphyllum*-type shoot seems to be an initial and rather common form. It is the dominant type in *Hirmeriella* (Harris 1979), and occurs in *Tomaxellia* (Archangelsky 1966), *Pseudofrenelopsis* (Watson 1977), and *Suturovagina*. The *Geinitzia*-type shoot is present in *H. crucis* (Kendall) as the juvenile shoot and becomes a predominant type of shoot in *Tomaxellia* (Harris 1979, p. 18; Archangelsky 1966, 1968). Decussate phyllotaxis characteristic of *Cupressinocladus* (Chaloner and Lorch 1960; Barnard and Miller 1976; Watson 1977) also exists in *H. crucis* (Harris 1979) and *Frenelopsis teixeirae* (Alvin and Pais 1978). The shoot with open-sheathed leaves predominant in *Suturovagina*, has been found in some species of
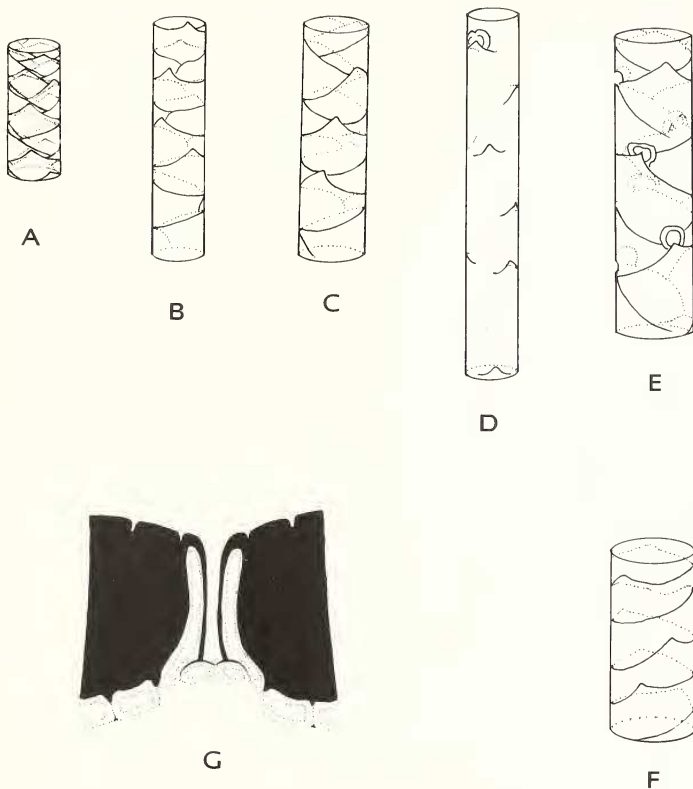
TEXT-FIG. 1. *Suturovagina intermedia* Chow and Tsao. A–F. Diagrammatical reconstructions of different types of shoots (all ×2). A, *Brachyphyllum*-type shoot (based on PB 10184). B, shoot type 2 (based on PB 10223); C, shoot with open-sheathed leaves above and leaves with suture below (based on PB 10210); D, shoot with scale leaves at intervals (based on PB 10212); E, shoot with open-sheathed leaves, showing branchlet scars (based on PB 10200); F, abnormal shoot with 'continuing' leaves (based on PB 10180); G, reconstructed transverse section of a stoma as that in Pl. 78, fig. 10 (right), ×200.

Pseudofrenelopsis (especially *P. varians* Fontaine; see Watson 1977). Thus, it is sometimes almost impossible to identify the genus when only a few isolated shoot fragments are available. I propose in the following key to separate the leafy shoots of different genera of Cheirolepidiaceae on the basis of the characters of their typical mature shoots.

1. Phyllotaxis spiral . . . . (2)
   Phyllotaxis decussate or whorled . . . . (6)
2. Leaf for the most part free from the stem . . . . (3)
   Leaf adpressed . . . . (4)
3. Leaf somewhat dorsoventrally flattened . . . . *Pagiophyllum* (*Hirmeriella*)
   Leaf equally thick in vertical and horizontal directions . . . *Tomaxellia, Geinitzia* (?*Hirmeriella*)
4. Leaf scale-like . . . . *Brachyphyllum* (*Hirmeriella*)
   Leaf encircling most or all of stem . . . . (5)
5. Leaf forming closed sheath . . . . *Pseudofrenelopsis*
   Leaf forming open sheath . . . . *Suturovagina*
6. Suture present between leaves . . . . *Cupressinocladus*
   Suture absent . . . . *Frenelopsis*

It is obvious that in some cases an accurate determination of leafy shoots, as well as their reference to the Cheirolepidiaceae, is possible only when cuticular structures and fructifications are known, especially those of *Hirmeriella*, *Tomaxellia*, and *Cupressinocladus* types.

Suturovagina intermedia Chow and Tsao

Pls. 75–77; Pl. 80, fig. 8; text-figs. 1A–G, 2A–J, 3A–C

1977   *Suturovagina intermedia* Chow and Tsao, p. 167, pl. 2, figs. 1–14; text-fig. 1.
1979   *Suturovagina intermedia* Zhou and Cao, p. 220 (name only).

Emended diagnosis. Juvenile shoots bear irregularly spaced, very loose spirally arranged scale leaves. The slender mature shoots (ultimate branchlets) either have broad scale leaves (usually only seen at the terminal and basal portions of the shoot) or more commonly comparatively longer open-sheathed leaves with either a gap or a suture between the two lateral edges. The more robust mature

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EXPLANATION OF PLATE 75

Figs. 1–27. *Suturovagina intermedia* Chow and Tsao; all figures are × 2.   1, isolated scale leaves of different shape and size, PB 10185–10198.   2, a branchlet showing upward transition from scale leaf to open-sheathed leaf with either a gap or a suture between the two lateral edges, PB 10171.   3, a branchlet with scale leaves at the base and open-sheathed leaves above, PB 10175.   4, a shoot with open-sheathed leaves showing two axillary buds of branchlets, PB 10201.   5*a, b*, two sides of a shoot showing open-sheathed leaves with either a gap or a suture between the two lateral edges, PB 10224.   6, a shoot showing a gradual upward transition from open-sheathed leaf to leaf with sutured, complete sheath, PB 10204.   7, 8, 12*a, b*, ultimate juvenile shoots bearing scale leaves at long intervals, PB 10217, 10218, 10219.   9, a broad juvenile shoot with inconspicuous scale leaves, PB 10220.   10*a, b*, 11*a, b*, two sides of the juvenile shoots with large leaves at short intervals, PB 10176, 10182.   13*a, b*, two sides of a shoot showing two branchlet scars and leaves with either a suture or a notch, PB 10165.   14*a, b*, two sides of a shoot showing complete-sheathed leaves with a notch, PB 10209.   15*a, b*, two sides of a shoot with 'continuing' leaves, PB 10181.   16, a fragment of a shoot with two successive branchlets, PB 10216.   17, a shoot showing imbricate leaves, some of them merging into the adjacent ones, PB 10178. 18, 23, 25–27, shoots of different dimensions with open-sheathed leaves. Note the longitudinal fissures on the cuticle of the broadest shoot in 26 and buds and scars of branchlets here and there, PB 10168, 10172, 10206, 10169, 10222.   19, apical part of a juvenile shoot showing short intervals between leaves, PB 10163. 20, branchlet showing the leaf interval becoming shorter towards the contracted basal part, PB 10213. 21, a shoot showing an abnormal suture on one of the open-sheathed leaves, PB 10177.   22, a juvenile shoot with ten leaves, only seven visible in the figure, PB 10202.   24, a broad juvenile shoot with large leaves at short intervals, PB 10167.

PLATE 75
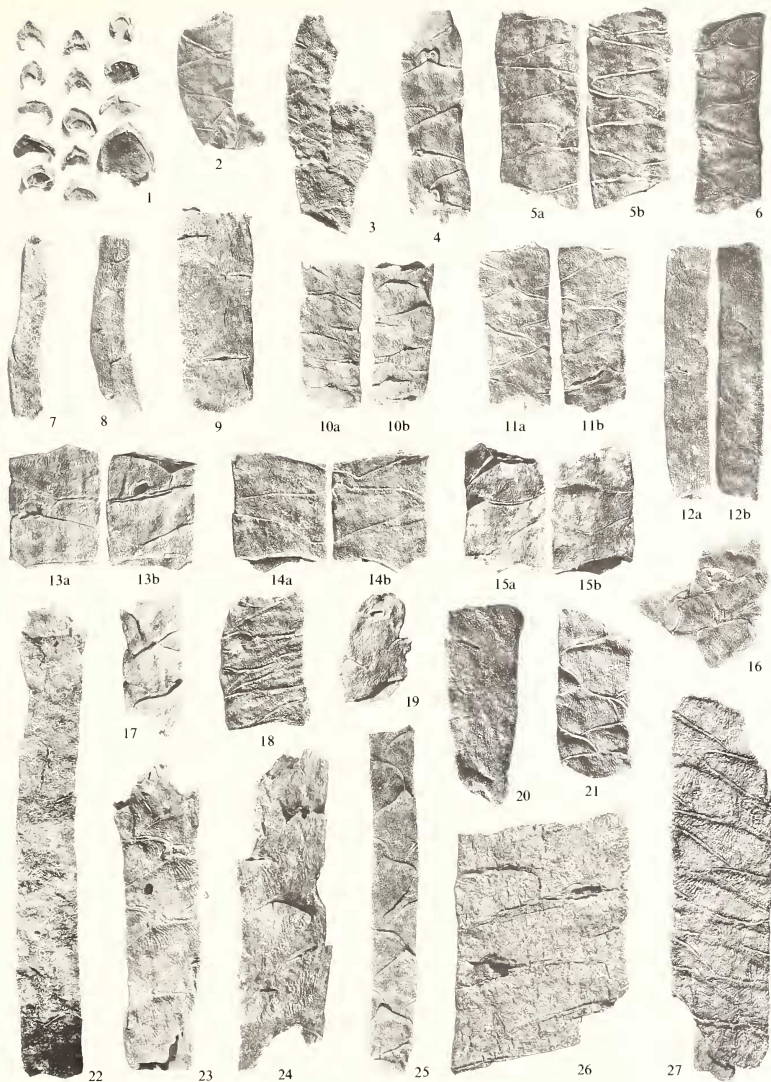
ones (main branchlets or branchlets of lower order) have comparatively short, open-sheathed leaves usually with a wide gap between the two lateral edges. Leaves with only the small, apical portion free, normally arranged in 2/5 (occasionally 3/7–3/8) loose spiral phyllotaxis. Leaf apex broadly acute, 90–120°. Adaxial side of leaves triangular to almost ring-shaped, usually short or undeveloped, but may reach three-quarters (or even equal) the length of some small scale leaves of the mature shoot. Abaxial side decurrent, with numerous roughly parallel grooves tending to converge towards the apex. Leaf upper margin entire, sometimes scarious and microscopically dentate, especially on the juvenile shoots. Cuticles of leaf very thick. Adaxial side composed mainly of elongated cells. $40-110 \times 20-70 \ \mu m$, arranged in longitudinal rows tending to converge towards the apex. Abaxial side up to 250 μm thick, with sunken stomata in the grooves, arranged in roughly longitudinal uniseriate files (sometimes biseriate at the lower part of leaf and more or less irregular on juvenile leaf); apex, margin, and base of leaf usually free from stomata. Juvenile shoot leaf base stomatiferous, merging uninterruptedly into the stem. Stomata elliptical to rounded in surface view, $40-150 \times 30-100 \ \mu m$ in diameter; guard cells $50-80 \times 15-30 \ \mu m$; apertures randomly orientated. Subsidiary cells normally eight (sometimes six to eleven) in number, of nearly uniform shape and size, round to elliptical in surface view and 10–30 μm in diameter, projecting upwards, up to 200 μm high, surrounding the stomatal pits, without a conspicuous papilla or hair on the periclinal wall. Encircling cells absent. Epidermal cells adjacent to stomata, usually differing slightly from the rest in shape and size. Epidermal cells normally larger than subsidiary cells in surface view, $10-60 \times 7-65 \ \mu m$, rectangular to polygonal, arranged in one to three longitudinal rows between each row of stomata. The epidermal cells in the stomatal rows are usually smaller and more irregular in shape. Anticlinal walls of cells straight. Periclinal walls smooth or sometimes slightly bulging. Compressed secondary xylem core one-third to two-thirds total width of shoot. Tracheids 7–12 μm in diameter, with crowded to sparse, uniseriate, elliptical to nearly round bordered pits, $6-8 \times 4-6 \ \mu m$ on the radial surface.

Description and discussion. The longest shoot seen is 165 mm long and incomplete. The most slender one is only 2 mm wide, while the widest reaches 20 mm. They vary considerably in having leaves of different shapes. Three main types of shoot were recognized:

　　1. Shoot bearing very loose spirally arranged scale leaves at intervals (text-fig. 1D).
　　2. Shoot bearing leaves encircling the stem with a complete sheath which is usually interrupted by a distinct suture (text-fig. 1B).
　　3. Shoot covered with broad scale-like to open-sheathed leaves (text-fig. 1A, E).

The longest shoot of type 1 so far obtained has ten leaves and is 47 mm long (Pl. 76, fig. 8). The leaves are small, triangular to crescent-shaped, with scarious margins. Their adaxial surface is usually of less than half the height of leaves and becomes indiscernible on the wide shoots. The interval between each two adjacent leaves (namely the vertical distance from the apex of a leaf to the base of the leaf above) varies according to their position on the shoot and the width of shoot on which they were borne. Normally, the interval between two leaves tends to shorten towards both ends of a shoot and the longer intervals occur in connection with the narrower shoots, but irregular intervals are sometimes present on the same shoot (text-fig. 2E).

Type 2 is represented in the material by comparatively fewer shoots which are of medium width (text-figs. 2C, I; Pl. 75, figs. 13a, b, 14a, b), no shoots being found less than 3·5 mm or more than 9 mm in diameter. The leaves are broad and encircle the axis laterally to form a complete sheath. A distinct suture is usually seen below a notch in the leaf margin. The adaxial side of the leaf is short and somewhat ring-shaped. The abaxial side is decurrent and normally slightly overlapped by the apical portion of the leaf below. The decurrent leaf base cushion is cylindrical with oblique ends. Normally, the height of the exposed part of a leaf matches the width of the shoot, but a slender shoot usually bears higher (longer) leaves and a broader shoot, shorter leaves.

The most common shoots in the debris belong to type 3. They display certain variations in the width of shoot as well as the shape of leaves. Slender shoots (3–6 mm; text-fig. 2A, B) usually bear
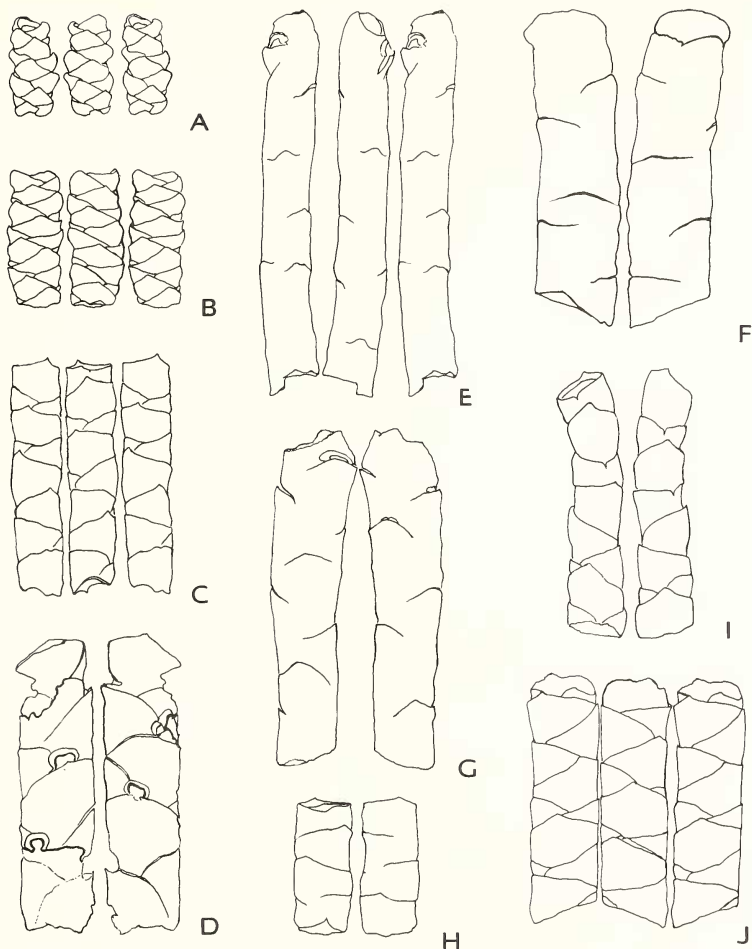
TEXT-FIG. 2. *Suturovagina intermedia* Chow and Tsao (all are ×2, showing both sides of compressed shoots; one side of the shoot is sometimes drawn twice in order to show the continuity of leaves on the two sides clearly). A, B, *Brachyphyllum*-type shoots belonging to the terminal portion of ultimate branchlet, PB 10183, 10184; C, shoot showing leaves with complete sheath interrupted by a suture, PB 10223; D, shoot with open-sheathed leaves and about six consecutive branchlet scars, PB 10200; E–H, shoots with scale leaves at intervals; E, G showing scars or buds of branchlets, PB 10212, 10221, 10199, 10207; I, most leaves having an inconspicuous notch-like suture, except for the basal two leaves which have a wide gap between the two lateral edges, PB 10211; J, the five leaves on the upper part of a shoot with an incomplete open-sheath, those on the lower part with a complete sheath interrupted by a suture, PB 10210.

broad scale-like imbricate leaves which encircle more than half the width of the stem. Stout shoots (4–20 mm; text-fig. 1D, J; Pl. 75, figs. 18, 23, 25–27) commonly bear overlapping open-sheathed leaves which enclose the large portion of the stem, leaving a gap between the two lateral edges. There exists, however, no line of demarcation between them. The adaxial surface of leaves is well developed and triangular to crescentic in shape. The leaf base cushions vary from crescentic to rhomboidal. The basal part of the abaxial surface of the leaf is often concealed. On some shoots the open-sheathed leaves are separated from each other, as the basal part of the leaf abaxial surface is exposed and merges into the stem (Pl. 75, fig. 6). Normally, the height (length) of a leaf is more or less equal to the width of the shoot on which the leaf was borne, but leaves are longer on a slender shoot and shorter on a robust shoot.

There is a series of transitional forms between shoots of type 2 and type 3 as well as those of type 3 and type 1. On a shoot of type 2, there may occur leaves with their two lateral edges nearly attached or separated by a narrow gap (text-fig. 2I; Pl. 75, fig. 5a, b). The reverse is the case in some shoots of type 3 (text-fig. 2J; Pl. 75, figs. 4, 6). These shoots, in fact, could be referred to either type 2 or type 3 with equal justification. In some shoots of type 1 (Pl. 75, figs. 10a, b, 11a, b, 24), the intervals between leaves tend to be shortened and the scale leaves become large and arranged in closer spiral. Such shoots come very near to some of the shoots of type 3 on which the leaves do not overlap but are separated from each other by intervals (Pl. 75, fig. 6). Although there are no direct links between shoots of type 1 and type 2, various shoots of type 3 could fill the morphological gap.

A few extremely unusual shoots (text-figs. 1F, 3B; Pl. 75, fig. 15a, b) were found in the debris after a careful search among thousands of specimens. They look as if they are 'segmented' as in *Frenelopsis* and *Pseudofrenelopsis*, but after close examination, I found surprisingly that the upper edges of leaves are continuous with those of the adjacent leaves above and below, to form a spiral line encircling the

TABLE I. Measurement of different types of shoots; values for the gross morphological data are based upon at least fifty measurements.

	Shoot with scale leaves at intervals	Shoot bearing complete sheathed leaves with a suture	Shoot with open-sheathed leaves	Shoot with imbricate scale leaves
Length of leaves	0·5–2 mm $m = 1·06$ mm, $\sigma = 0·43$	3–9 mm $m = 4·92$ mm, $\sigma = 1·39$	2·5–10 mm $m = 5·3$ mm, $\sigma = 1·62$	2–6 mm $m = 3$ mm, $\sigma = 0·98$
Breadth of shoots	2–15 mm $m = 5·3$ mm, $\sigma = 2·45$	3·5–9 mm $m = 5·16$ mm, $\sigma = 1·57$	4–20 mm $m = 6$ mm, $\sigma = 3·38$	3–6 mm $m = 4·26$ mm, $\sigma = 0·84$
Interval between leaves	1–15 mm (occasionally leaves overlap)	Leaves slightly overlap		Leaves overlap
Ratio of length of leaf to width of shoot	One-thirteenth to two-thirds	Half to one and three-quarters	Half to two	Half to two
Size of stomata (outside view)	75–100 × 40–60 μm (On robust shoot 40–50 μm in diameter)	50–80 × 40–60 μm	40–70 × 25–30 μm (On robust shoot 100–120 μm × 60–80 μm)	40–100 × 40–65 μm
Size of stomata (inside view)	90–125 × 60–100 μm (On robust shoot 100–180 × 70–100 μm)	50–100 × 30–60 μm	40–100 × 40–60 μm (On robust shoot 80–120 × 50–100 μm)	50–100 × 60–80 μm
Density of stomata	24–36/mm² (On robust shoot 16–20/mm²)	40–50/mm²	32–56/mm² (On robust shoot 14–20/mm² inside view, 4–7/mm² outside view)	64–130/mm²
Size of epidermal cells	15–60 × 30–65 μm	15–60 × 30–60 μm	10–40 × 15–70 μm	7–30 × 10–40 μm

stem. Perhaps such a kind of shoot is an abnormal variant, as specimens are very rare, only two fragments being so far found. On rare shoots of type 3 (text-fig. 3c; Pl. 75, fig. 17), there are a few leaves which tend to merge into the adjacent ones by a shortening or vanishing of lateral edges.

The great variation in leafy shoots, which we encountered in the material, suggests that we are dealing with a heterophyllous conifer. Shoots of type 3 have a great range in width, and are therefore thought to represent shoots on different positions of the plant. The most slender ones have the usual *Brachyphyllum* aspect. No branched specimens of this kind have been found. Presumably, they represent the ultimate branchlets or the terminal portions of the ultimate branchlets. The broadest shoot of type 3 so far found in the debris attains 20 mm in breadth; it is characterized by short open-sheathed leaves covered with very tough cuticle. The leaves usually have conspicuous longitudinal fissures on their surface (Pl. 75, fig. 26; Pl. 76, fig. 7), which suggest a tangential expansion of the shoot due to subsequent growth. I believe, therefore, that such robust shoots with short leaves represent the main branchlets. There are transitional forms of which the shoots and leaves are intermediate in thickness and shape respectively between the two extremes. Those slender shoots with longer leaves are considered to be ultimate or penultimate branchlets, while those broader shoots with shorter leaves are thought to belong to branchlets of lower order.
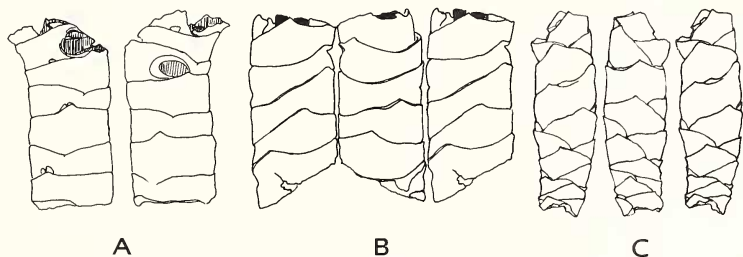
TEXT-FIG. 3. *Suturovagina intermedia* Chow and Tsao (all are × 2; both sides of the compressed shoots are shown, one side of shoots in B and C being drawn twice). A, a shoot with scars and buds of branchlets, PB 10170; B, an abnormal shoot with 'continuing' leaves and a compressed xylem core, PB 10180; C, a shoot with imbricate scale leaves bearing some abnormal 'continuing' leaves in the middle part, PB 10179.

Shoots of type 2 are few in number and have a rather limited width range in comparison with those of type 3. It seems that type 2 has not been an important variant of the shoot on the plant but occurs mixed with type 3 on certain branchlets (most probably penultimate ones). No shoots which could be regarded as ultimate or main branchlets have been found.

Like type 3, type 1 has a complete series of shoots of its own (Pl. 75, figs. 7–12b, 20, 22) which cover a range of width of 2–15 mm. Although there are intermediate forms between types 1 and 3, their typical forms never seem to occur on the same branch. Since type 1 includes the most slender shoots with the longest leaf interval and since these shoots are scarcely branched and have leaves with thinner cutinized cell walls compared with those of similar width of other types, I am inclined to regard type 1 as the shoot of the juvenile tree or the newly formed shoot of the mature tree, such as in some extant conifers (e.g. *Juniperus chinensis* L.). It is also worth mentioning that, on the surfaces of leaves of the broadest specimen of type 1, longitudinal fissures like those of the broadest mature shoot do not exist.

Despite the great variation in gross morphology of shoots, the cuticular structures of leaves are essentially similar. The variation in details of the cuticle is mainly associated with the age of shoots and the state of preservation. The outlines of epidermal cells are more clearly seen on the inner side of
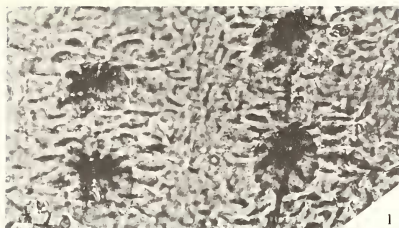
the leaf cuticle. In outside view, they are often obscure, especially in juvenile and old shoots, which might be due partly to presence of the outermost wax layer. Their periclinal walls are normally more or less bulging and smooth in surface view, but occasionally have a papilla (Pl. 77, fig. 5). The anticlinal walls are thin (1–3 μm wide) in leaves of most juvenile shoots, but much thicker (commonly 5–10 μm wide) in leaves of mature shoots. In the leaves of robust juvenile shoots, the anticlinal walls of cells are also thickened and the lumina of cells are very narrow (Pl. 76, fig. 5). The size of epidermal cells and stomata normally decreases in leaves of mature and robust shoots. The density of stomata, however, which varies to a certain extent within a single leaf (higher in lower part where stomata are biseriate), tends to be higher in most mature shoots, though lower in robust shoots (Table 1). Leaves of old and robust shoots with tough cuticle often have very sparse stomata on the outer surface because of the presence of longitudinal fissures between files of stomata (Pl. 76, fig. 7), though stomata are more frequent on the inner surface of the cuticle. Hypodermal cells have not been seen on leaf cuticles except some possible traces of cell wall on some cuticle of certain juvenile shoots (Pl. 77, fig. 8).

The most characteristic feature of the cuticles is the structure of the stomata, which remains unchanged on leaves of all types of shoots. Most of the stomata examined have lost their guard cells. More or less well-preserved guard cells were only seen on leaves of the juvenile shoots. The distal walls of subsidiary cells are as a rule strongly cutinized, while the radial and proximal walls were not preserved on most of the leaves studied.
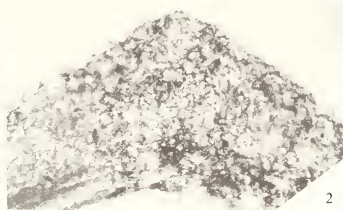
Branched shoots are not common in the debris. This may be partly due to the maceration which dismembered the shoots. In hand specimens, shoots longer than 10–15 cm are not uncommon, but again most of them are unbranched. Almost all the branched shoots studied are more than 4 mm wide. They show normal axillary branching like that in *Pseudofrenelopsis parceramosa* (Watson 1977, Pl. 85, fig. 3; Alvin and Hlůstík 1979, pp. 239–240, text-fig. 15), but no whorled branching such as that observed by Alvin in *P. parceramosa* (pers. comm.) has been seen. The branchlets arise immediately above the subtending leaves on the parent shoot. Initially, a pair of small leaves emerges (Pl. 75, figs. 4, 23; text-figs. 2G, 3A), which are of about the same size and laterally symmetrical to each other, though occasionally asymmetrical. Sometimes there may be one or three leaves instead of two. These two leaves which cover the base of the branchlet afterwards (Pl. 75, fig. 3), are always shorter and smaller than the succeeding leaves on the branchlet and are of the same shape on different types of shoots. The branchlets (or branchlet scars and buds) which always contract at the bases, are carried at rather irregular intervals on the shoots. One shoot (text-fig. 2D) has been found to have at least six successive, spirally arranged branchlet scars, but others show branching intervals of one to many (up to more than twenty) leaves. When branched sparsely, the shoot often shows an appearance of alternate branching in one plane (Pl. 80, fig. 8). As there are no specimens which are large enough to show the whole branching system, it is almost impossible to ascertain whether different intervals of branching occur on the same shoot or not. It appears, however, that this is likely, as the leaves are
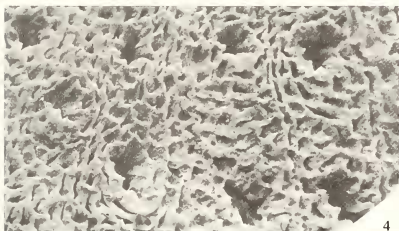

PLATE 76

ZHOU, cheirolepidiaceous conifer

sometimes also carried at very different intervals on the same shoot (text-fig. 2E). The branched shoots which are of very different thickness and with different ratios of leaf height to width of shoot, may suggest a fairly complicated, repeated branching. Perhaps, *Suturovagina intermedia* had a branching system similar to that of *Frenelopsis ramosissima* Fontaine (Fontaine 1889, Pls. 95–100; Watson 1977, Pls. 93, 94), although branching was far more sparse, especially in the juvenile shoot.

Little is known about the structures of the compressed xylem core of the shoots, as many specimens studied are structureless. Only a few show outlines of tracheids on the transverse and radial sections, and one, belonging to a 17 mm broad leafy shoot, shows bordered pits on the radial walls of tracheids (Pl. 78, fig. 5). No elements other than trancheids have been identified, though traces of ray cell walls have been seen on the radial fractures of some specimens.

Comparison. In addition to the type-species, there are at least two other forms described from different formations of China as *Brachyphyllum obtusum* and *Manica tholistoma* (Chow and Tsao 1977; Zhou and Cao 1979), which should perhaps be referred to *Suturovagina*. Both are similar to *S. intermedia* in many respects, especially in stomatal structures, but they are different in some details. *B. obtusum* is represented by a single *Brachyphyllum*-type shoot which is, however, distinguished by having obtuse leaves, a feature not known in any shoots from the present abundant material. The adaxial cuticle is also characteristic as the epidermal cells are smaller and more or less isodiametric. All the shoots referred to *M. tholistoma* look like those of *S. intermedia* with complete-sheathed leaves without a suture (Pl. 75, figs. 14*a*, *b*), but the type specimen of *M. tholistoma* (Chow and Tsao 1977, Pl. 5, figs. 1–2) shows more marked surface grooves and larger, more crowded stomata in comparison with the mature shoots of *S. intermedia*. It is not certain whether the two forms (especially *M. tholistoma*) actually represent distinct species, because some of the differences are of little taxonomic importance, particularly if we take the great variation of cheirolepidiaceous conifers into consideration. As no other types of shoot nor the variation of cuticular structures are known, a closer comparison and further discussion are at present impossible. I would keep them separate from *S. intermedia* for the time being until more specimens are available for examination.

Secondary xylem

Associated fusainized and compressed wood specimens have been studied under SEM and the light microscope. Two different forms of secondary xylem have been recognized, chiefly based on the information obtained from fusain. Both are composed of tracheids with parenchymatous rays. One form, characterized by spiral thickening(?) in tracheids and one to two superimposed large bordered pits in the cross field, was regarded as representing a gymnosperm of a quite different taxon. Another form has been considered to belong to *S. intermedia* and is described below. The evidence of attribution of this dispersed secondary xylem consists in the close association with leafy shoots and in the similarity in tracheids to the compressed xylem of some corticated leafy shoots. (Cf. Pl. 78, figs. 4,

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Figs. 1–10. *Suturovagina intermedia* Chow and Tsao; all are SEM photographs. 1, outside view of a stoma from the cuticle of a robust juvenile shoot, × 400. PB 10235. 2, outside view of a stoma from a leaf of shoot type 2, × 400. PB 10230. 3, outside view of a stoma from a juvenile shoot, outlines of epidermal cells not seen, × 400. PB 10218. 4, inside view of a stoma showing hollow subsidiary cells which are smaller than the normal epidermal cells, × 400. PB 10233. 5, outer surface of an adaxial cuticle showing papillae on some epidermal periclinal walls, × 400. PB 10232. 6, stoma in inside view, showing the guard cells, × 700. PB 10228. 7, adaxial side view of an adaxial cuticle, × 400. PB 10241. 8, possible trace of hypodermal cell walls seen on the inner surface of a stem cuticle from a juvenile shoot, × 400. PB 10233. 9, a stoma in transverse section (from the leaf on a *Brachyphyllum*-type shoot) showing the vertical extension of subsidiary cells and the more or less funnel-shaped upper part of stoma, × 400. PB 10229. 10, transverse section of stomata (from a juvenile leaf) showing the guard cells deeply sunken at the bottom of the stomatal pits, × 200. PB 10228.

PLATE 77

ZHOU, cheirolepidiaceous conifer
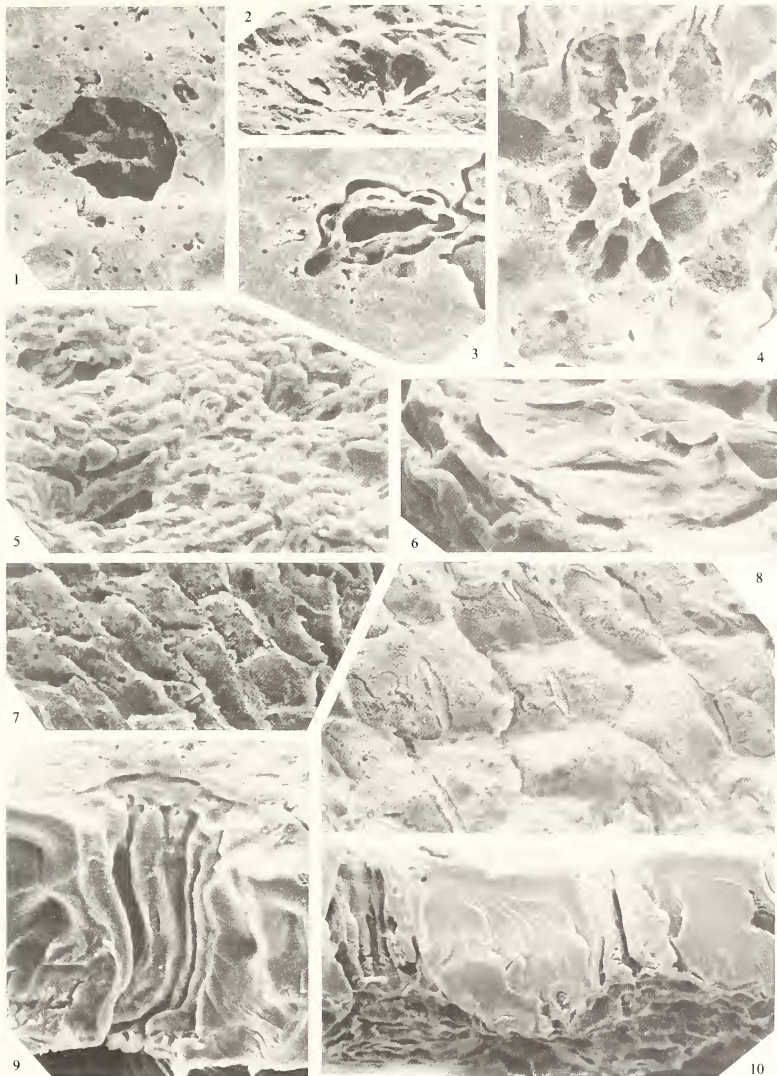
8 with Pl. 78, fig. 5.) In the debris obtained, about 95% of fossil fragments are of *Suturovagina*, and no other macrofossils are known to have comparable tracheids. The close resemblance in structure between the present secondary xylem and the secondary xylem already proved to belong to other Cheirolepidiacous conifers (see below) also supports the attribution.

Description. Transverse section (Pl. 78, figs. 1, 3): the secondary xylem is compact and consists of tracheids and parenchymatous rays only. The growth rings are distinct and of various widths from 150 to 850 μm. The early wood is formed by a broader zone of tracheids with larger lumina. The late wood is composed of a narrower zone (four to six cells only) of tracheids with narrower lumina. In cross-section, the tracheids are rectangular to polygonal, $10-26 \times 8-30$ μm in the early wood and $5-10 \times 15-25$ μm in the late wood. Their walls vary from 1 to 7 μm in thickness. There are about 2,000–3,000 tracheids per square millimetre in the early wood. The septate tracheids are present occasionally in the late wood. No resin ducts or cysts have been detected.

Tangential section (Pl. 78, fig. 2): the tangential surfaces of tracheids are only rarely pitted. Pits are small (about 10 μm in diameter), bordered, and form short, contiguous single rows. The parenchymatous rays are overwhelmingly uniseriate and low, one to nine (mostly less than four to five) cells high. There are about forty-five to eighty rays per square millimetre. The ray cells are usually slightly elongate, about $12-30 \times 10-20$ μm in size, with thin horizontal walls.

Radial section (Pl. 78, figs. 4, 6–8; Pl. 79, figs. 1–2): the bordered pits are arranged in single, contiguous or sparse rows on the radial walls of tracheids, but sometimes, the tracheids are not pitted for the large part. Pits are $10-15$ μm in diameter, with an elliptical to almost rounded aperture, $5-8 \times 2\cdot5-4\cdot0$ μm in size. The rays consist entirely of parenchymatous cells with thin and smooth transverse and tangential walls. No pitting is seen on the horizontal and tangential walls. The cross fields are rectangular, $12-22 \times 10-25$ μm, either vertically or more often transversely elongated. There are normally four to six (range two to eight) cupressoid pits arranged in one to three horizontal rows in each field, which are broadly elliptical to rounded in outline, $4-6 \times 3\cdot5-6\cdot0$ μm in size, separated from each other or slightly contiguous. The apertures are elliptical, $2\cdot5-4\cdot0 \times 1\cdot5-2\cdot0$ μm and obliquely orientated in the same direction. No vertical wood parenchyma has been found, nor any trace of resinous tracheids.

Remarks. The above description was based on several well-preserved small pieces of fusain of twigs, the largest of which is estimated at 2 cm in diameter (partly shown in Pl. 78, fig. 1). Many slender dispersed compressed wood cores (most of them, in fact, being decorticated shoots) have also been studied, and proved to be essentially similar in structure. They have a similar number of cupressoid pits in the cross field. The secondary xylem pitting is of the same 'mixed' type, though alternative biseriate bordered pits sometimes occur. These are, however, not figured because the material was not so well preserved as the fusain.

On the transverse section of the late wood, horizontal cross walls are seen on occasional tracheids which have been, therefore, interpreted as septate. However, I failed to prove the existence of septate tracheids on the radial and tangential sections.

EXPLANATION OF PLATE 78

Figs. 1–8. Secondary xylem; all are SEM photographs and from PB 10242, unless otherwise stated. 1, transverse section, showing irregular growth rings, $\times 50$. 2, tangential fracture, showing the low rays and pitting on some tracheids (upper left), $\times 100$. PB 10243. 3, as 1, showing the transverse walls in a few tracheids of the late wood and amorphous deposit in the ray cells, $\times 400$. 4, radial surfaces of tracheids showing either sparse or crowded bordered pits, $\times 1000$. 5, radial fracture of the *in situ* compressed secondary xylem from PB 10169, showing pitting on tracheids, $\times 2000$. 6, pits of 'vestured' appearance in a cross field, $\times 5000$. 7, cross fields with crowded cupressoid pits, $\times 2000$. 8, radial fracture showing ray cells, cross fields, and tracheids with bordered pits, $\times 400$. PB 10243.

PLATE 78

ZHOU, cheirolepidiaceous conifer
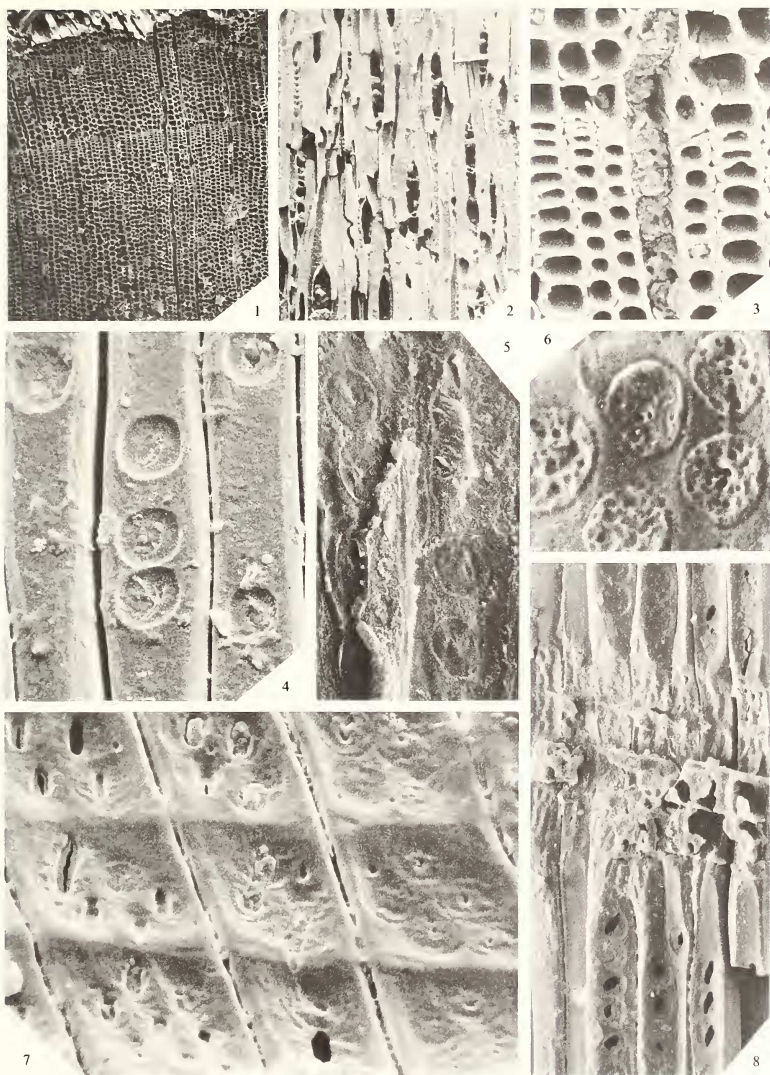
The ray cells are usually represented by cavities separated by thin transverse walls on the tangential section. Occasionally, they are filled with amorphous material (resin?). They are probably uniseriate throughout. Some wide gaps shown on the tangential surface suggest possible biseriate rows in the middle of rays, but they may represent distended or distorted ones formed by charring (Harris 1957, pp. 295–296).

The pits in the cross fields normally have smooth and flat borders, but pits of a 'vestured' appearance are also occasionally present (Pl. 78, fig. 6).

The presence of uneven growth rings, which occur usually in traumatic wood, is of interest as it is not inconsistent with the irregular intervals between leaves (and probably branchlets too) on some shoots of *Suturovagina*. A similar phenomenon has also been noticed by Alvin *et al.* (1981) on *Pseudofrenelopsis parceramosa*. They believed that it may well be related to periods of drought when growth was interrupted.

The similarity in structure between tracheids of the dispersed fragments of fusain described above and those of the compressed corticated shoots has already been mentioned. The only difference known is the smaller size of bordered pits and tracheids in the compressed woods. This, however, might be expected between a slender and a broader twig.

Comparison. I can find no important differences between the specimens of secondary xylem under discussion and those of some other members of Cheirolepidiaceae. All of them belong to *Protopodocarpoxylon* or *Protocupressinoxylon* which are characterized by 'mixed' pitting on the tracheids, parenchymatous rays, and podocarpoid to cupressoid pits in the cross field.

The secondary xylem of material from the Rhaeto-Liassic of South Wales, referred by Harris (1957) to *Cheirolepis* (= *Hirmeriella*) *münsteri*, has similar pitting on the tracheids and similar rays (one to eight cells high), but the growth rings are inconspicuous and the cross fields which contain a similar number (three to eight) of pits are usually longitudinally elongated.

Protopodocarpoxylon aveiroense Lauverjat and Pons 1978, a secondary wood from the Senonian of Portugal that is believed to belong to *Frenelopsis oligostomata* Romariz, differs only in detail from the present form. The growth rings are distinct but the late wood is narrow and inconspicuous. The tracheids are larger so that there are less tracheids (830–1,450) per square millimetre in the transverse

TABLE 2. Comparisons between secondary xylems referred to different members of Cheirolepidiaceae.

	Hirmeriella münsteri (from S. Wales)	*Frenelopsis oligostomata* (*Protopodocarpoxylon aveiroense*)	*Pseudofrenelopsis parceramosa*	*Suturovagina intermedia*
Growth ring	Inconspicuous	Present	Distinct but uneven	Distinct but uneven
Number of tracheids per mm² in transverse section	—	About 830–1,450	About 520 (silicified specimen), 1,250 (fusain)	About 2,000–3,000 (fusain)
Pitting of tracheid	'Mixed' type	'Mixed' type	'Mixed' type	'Mixed' type
Septate tracheid	Unknown	Absent	Present	Present
Resinous tracheid	Unknown	Present	Present	Unknown
Shape of cross field	Square to longitudinally elongated	Longitudinally or horizontally elongated	Square to slightly elongated horizontally	Longitudinally or horizontally elongated
Number of pits per cross field	About 4 (range 3–8)	1–13	4–10 (range 1–17)	4–6 (range 2–8)
Parenchymatous ray	Probably all uniseriate, 1–8 cells high	Most uniseriate, 1–16 cells high	Mainly uniseriate, 1–14 cells high	Probably all uniseriate, 1–9 cells high
Number of rays per mm² in tangential section	—	35–50	30 (silicified specimen) 60 (fusain)	About 45–80 (fusain)
Resinous ray cell	Unknown	Present	Present	Probably present

section. The rays are somewhat higher (up to ten to sixteen cells) and there are more pits in the cross fields. I cannot confirm the presence in the Chinese wood of similar specialized, narrow resin cells as in the rays of *P. aveiroense*, though some of the ray cells, as mentioned above, might be resinous. Septate tracheids, however, are unknown in the Portuguese wood.

The wood of *Pseudofrenelopsis parceramosa* Fontaine (Alvin *et al.* 1981) from the Barremian of England has much in common with the wood described here. Both have distinct but uneven growth rings and occasional septate tracheids in the late wood. Their tracheids, rays, and cross fields are similar to each other. The differences lie only in the number and dimension of cells and pits. The tracheids of the English wood are larger, and there are more pits in the cross field and cells in the ray. A possible substantial difference is the absence of convincing resinous tracheids in the Chinese wood.

Alvin *et al.* (1981, p. 774) have summarized the occurrences and structures of the secondary woods of cheirolepidiaceous conifers. Their work shows that all the secondary woods having such an affinity, known from several different geological ages in Euramerica, have many features in common. This also applies to the secondary xylem here described from the Cretaceous of China. It is noteworthy that the structures of the secondary xylem of different members of Cheirolepidiaceae underwent very little change from Rhaetian to Maastrichtian times, although their leafy shoots display a great diversity in external morphology.

Associated male cone

Genus *Classostrobus* Alvin, Spicer and Watson 1978
Classostrobus cathayanus sp. nov.

Pl. 79, figs. 3–7; Pl. 80, figs. 1–7; text-fig. 4A, B

Diagnosis. Male cone borne on a short pedicel of 8 mm wide and 8 mm long (not complete), covered with broad leaves. Cone probably spherical, more than 20 mm long (apex not preserved) and 23 mm wide in the middle part. Microsporophylls borne spirally, with probably 2 + 3 parastichies, consisting of a slender stalk and a rhomboidal sporophyll head 7–10 mm high, 7–8 mm wide (exposed part 6–7 mm long and 4–5 mm wide). Apex acuminate. Abaxial cuticle of sporophyll head thick, consisting of polygonal cells, 40–60 × 15–25 μm in size; anticlinal walls 3–10 μm thick; periclinal walls with a large conical papilla usually 15–37 μm long, but longer near margin. Cutinized hypodermis present, consisting of elongated cells, 25 to > 100 μm long and 7–20 μm wide. Stomata not seen. Adaxial cuticle thinner, composed of elongated cells 40–90 × 8–30 μm, anticlinal walls thin (1–8 μm)
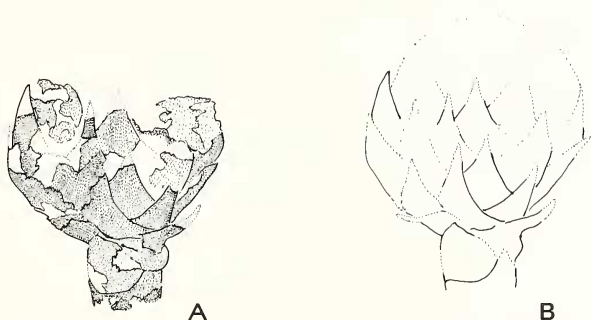
TEXT-FIG. 4. *Classostrobus cathayanus* sp. nov. (all are × 2). A, holotype PB 10237, the same as Pl. 81, fig. 1; coaly substance shown by stippling; B, the same, stippling being omitted in order to show the shape of sporophylls clearly.

and straight; periclinal wall smooth. Stalk of sporophyll with very delicate cuticles, consisting of elongated cells about 10 μm wide. Pollen sacs situated in the basal part of the sporophyll. Membrane thin and delicate, with isodiametric cells, 10–24 μm in diameter.

Pollen of *Classopollis*-type, spheroidal with flattened poles, 26–41 μm in diameter (mean = 33·28, s.d. = 3·57; thirty-five grains measured) in polar view, with a subequatorial circular furrow (rimula) situated at the distal edge of an equatorial band of about 7–8 μm in width; striations faintly developed, 5–7 rows in the band. Distal pore (cryptopore) round, 6–9 μm in diameter. Proximal tetrad mark distinct; laesurae 2–8 μm long. Exine 1·0–1·5 μm thick with grumous-verrucose or occasionally echinulate external sculpture; inner surface smooth or nearly so.

Name. Cathay, a poetical name for China.

Remarks. Like many fossil male cones, *Classostrobus cathayanus* is incompletely known, but its generic determination seems to be certain as characteristic *Classopollis* pollen grains have been found *in situ*. Only two specimens have so far been found, both being incomplete and partly pyritized. The type specimen (Pl. 80, fig. 1) seems to have lost its apical portion. The arrangement of sporophylls suggests, however, that most parts of the cone are undistorted. Almost all the information about this species was obtained from this specimen. The other (not figured) was sacrificed for transfer preparation, but little information has been added. Neither intact pollen sacs nor pollen masses were found. The pollen sacs seem to have shed their pollen and only a few preparations from the lower part of the sporophylls yield fragments of pollen sac membrane with some adhering pollen grains. It is not possible to determine the number and exact position of the pollen sacs on the sporophyll.

No well-preserved specimen of sporophyll with a complete stalk still attached has been found in the debris. A fragment of sporophyll with a short stalk of about 1 mm long, still attached, was obtained. The attachment of pollen sacs on the sporophyll, however, is not shown on this specimen. The cuticle of the stalk is very thin. Usually, it dissolves in ammonia. Only one preparation shows the outline of the elongate cells (not figured).

The abaxial surface of the sporophyll is covered with papillate thickening. Outlines of epidermal cells can only be seen on the inner side of the cuticle. No convincing stomata were found in spite of prolonged searching. The abaxial cuticle of a leaf on the pedicel has almost the same structure (Pl. 79, fig. 5).

The exine of pollen consists of only one layer, nothing like a nexine being seen in the slides.

Comparison. C. cathayanus which, if interpreted correctly, attains a size of more than 20 mm long and 23 mm wide, is the largest male cone so far known to me amongst Cheirolepidiaceous conifers. It also has the largest sporophylls which are distinguished from those of most male cones known of this extinct family by having a long and acuminate apex, instead of a short and broadly acute one (Archangelsky 1968; Barnard 1968; Muir and van Konijnenburg-van Cittert 1970; Hluštík and Konzalová 1976; Chow and Tsao 1977; Pons 1979). The cuticular structures of sporophylls, however, are essentially similar to each other in having a thick epidermal cuticle with well-developed cutinized

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EXPLANATION OF PLATE 79

Figs. 1–2. Secondary xylem; all are SEM photographs and from PB 10242. 1, two cross fields showing two and six bordered pits respectively, × 3000. 2, radial fracture showing the ray cells and pits in the cross fields, tracheids of the late wood on the left of the figure, × 400.

Figs. 3–7. *Classostrobus cathayanus* sp. nov.; all are from PB 10237; 3 and 6 are light micrographs. 3, abaxial cuticle of a sporophyll showing elongated hypodermal cells and polygonal epidermal cells with conical papillae, × 500. 4, outer surface of the abaxial cuticle of a sporophyll, showing conical papillae, × 700. 5, inner surface of the abaxial cuticle of a leaf on the pedicel, showing polygonal epidermal cells and elongated hypodermal cells, × 500. 6, adaxial cuticle of a sporophyll showing more or less elongated cells, × 500. 7, fragment of the membrane of a pollen sac with isodiametric cells and one adhering pollen grain, × 700.

PLATE 79

ZHOU, cheirolepidiaceous conifer
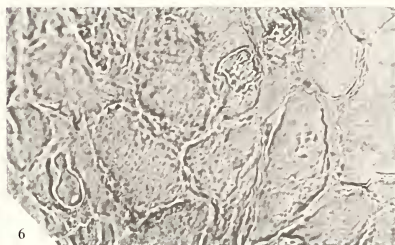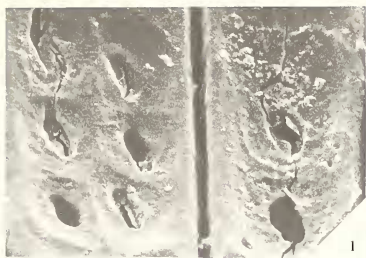
hypodermis and a thinner adaxial cuticle. The abaxial cuticles of *C. cathayanus* recall especially those of *C. comptonensis* (Alvin *et al.* 1978), in having conical papillae on the periclinal walls, though no stomata were seen. The adaxial cuticles of the two species are different. No papillae have been seen on the periclinal wall of those of the present species.

There is a general similarity in appearance between the pollen grains of *C. cathayanus* and those of the other members of the Cheirolepidiaceae. In respect of their size and their feeble equatorial striations, the pollen grains resemble those of *Brachyphyllum crucis* Kendall (van Konijnenburg-van Cittert 1971, 1972; Harris 1979), *B. scotti* (Kendall 1949), and *Frenelopsis oligostomata* Romariz (Pons and Brouton 1978), but the external sculpture is somewhat different. Internal sculpture of the pollen of *C. cathayanus* is scarcely visible, if present at all. The pollen grains described here might also be compared with some dispersed *Classopollis* species with weakly developed internal sculptures and striations, such as *C. simplex* and *C. keiseri* (Reyre 1970), but they are distinguished by their size and external sculptures.

Attribution. Though a direct connection has not been proved, I am convinced that *C. cathayanus* belongs to *Suturovagina intermedia*, because the latter is the only conifer which could be a *Classopollis*-producer that has so far been found in the material. As no stomata have been seen on the cuticles of the sporophyll and the leaf on the pedicel, an identity in cuticular structure between the cone and the leafy shoot cannot be established. The hairy epidermal cells of the sporophyll differ also very much from those of *S. intermedia* in appearance. Such differences, however, might be expected between a sporophyll and an ordinary leaf of a conifer. As is known, Cheirolepidiaceae male cones sometimes do have very sparse or even no stomata on the abaxial cuticle of the sporophylls (Alvin *et al.* 1978; Harris 1957). The hairy epidermis is a rather common phenomenon of cone scale of conifers, especially the female cone scale, e.g. *Cedrus deodara*.

GENERAL DISCUSSION

A revised study of *S. intermedia* based on the newly collected abundant material has revealed the following main points:

1. The shoots vary considerably in the shapes of their leaves. The mature shoot bears mainly broad leaves encircling the large part or the whole of the stem with either a gap or a suture between the two lateral edges. The shoot believed to represent the juvenile one bears scale leaves at intervals. Abnormal shoots with continuing spiral leaves have also been noted.

2. The cuticular structures of the leaf display no great variation in different shoots. The characteristic stomata differ from those of all other genera so far known in Cheirolepidiaceae.

3. The dispersed fossil secondary xylem shares all the common features of some other members of this family. The attribution of it to *S. intermedia* is based on the close association and the similarity in tracheids between the dispersed and *in situ* secondary xylem.

4. The associated male cone referred to *S. intermedia* yields *Classopollis* pollen, though continuity has not been demonstrated.

EXPLANATION OF PLATE 80

Figs. 1–7. *Classostrobus cathayanus* sp. nov.; all are from PB 10237; 2, 3, 5–7 are SEM photographs. 1, holotype, ×4 (in paraffin). 2, group of pollen grains, ×700. 3, distal view of a pollen grain, showing the subequatorial circular furrow and the round pore, ×*c.* 2000. 4, a pollen grain showing faintly developed striations, ×*c.* 1500. 5, a tetrad, ×1300. 6, part of a pollen grain in proximal view, showing strand-like elements in the triradiate slit, ×2000. 7, part of a pollen grain showing rimula and the surface sculpture, ×5000.

Fig. 8. *Suturovagina intermedia* Chow and Tsao; branched hand specimen, ×1 (in paraffin). PB 10238.

PLATE 80
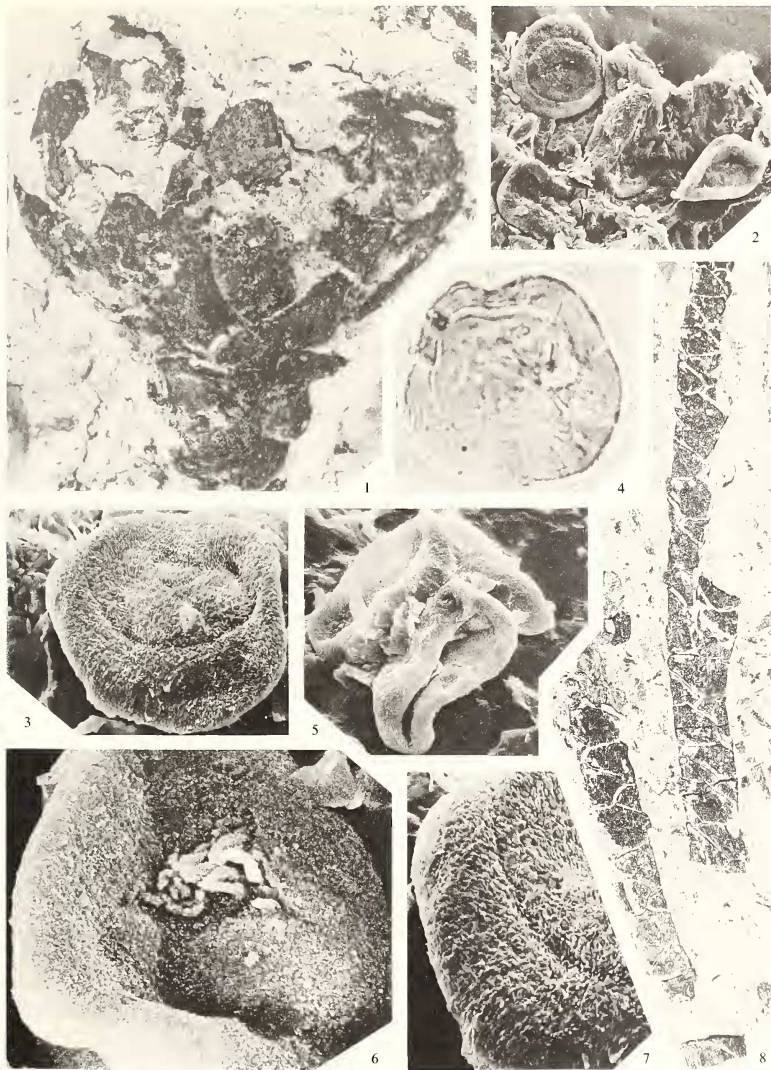
ZHOU, cheirolepidiaceous conifer

If, as I believe, all the above interpretations are correct, *S. intermedia* is a rather completely known Cheirolepidiaceous conifer which shows great variation in external morphology of leafy shoots. It is of interest that some types of these leafy shoots are unknown to me in any other conifers both living or fossil, although the secondary xylem and *Classopollis*-producing male cone are conventional in Cheirolepidiaceae. Alvin *et al.* (1978, p. 854) believe that the external morphological diversity of leafy shoot of different genera might well imply ecological diversity. The great morphological variation as well as overlap in characters between different genera suggests that during Jurassic and Cretaceous times Cheirolepidiaceae was a developing rather than a declining family.

Since fusain (fossil charcoal), as now accepted by many palaeobotanists, is a common product of natural wild fire (heath or forest fire) (Harris 1957, 1958; Batten 1974; Scott and Collinson 1978; Cope and Chaloner 1980; Alvin *et al.* 1981), its occurrence in the material indicates that the conditions in the Cretaceous of that part of China were sometimes favourable to the occurrence of wild fires. The distinct growth rings of secondary xylem suggest periodic droughts in which lightning was likely to occur.

So far, little is known about the shape and size of the whole *S. intermedia* plant. No well-preserved female cones were found in our material. The organization of the male cone still remains unclear and there is no direct evidence of the connection of the male cone to the leafy shoot. These gaps in information are expected to be filled in by further collection and study.

Cheirolepidiaceous conifers, so far as the present knowledge goes, are widely distributed in East China. From most localities, however, only a few specimens were collected, and these have not been carefully studied. It is to be hoped that these deficiencies will be made good by future work. The investigation of Cheirolepidiaceous conifers in this part of the world would certainly be helpful in forming a complete picture of the distribution, ecology, and evolution of this important, extinct family of Mesozoic conifers.

REFERENCES

ALVIN, K. L. and HLUŠTÍK, A. 1979. Modified axillary branching in species of the fossil genus *Frenelopsis*: a new phenomenon among conifers. *Bot. J. Linn. Soc.* **79**, 231–241.

—— and PAIS, J. J. C. 1978. A *Frenelopsis* with opposite decussate leaves from the Lower Cretaceous of Portugal. *Palaeontology*, **21**, 873–879.

—— FRASER, C. J. and SPICER, R. A. 1981. Anatomy and palaeoecology of *Pseudofrenelopsis* and associated conifers in the English Wealden. Ibid. **24**, 759–778.

—— SPICER, R. A. and WATSON, J. 1978. A *Classopollis*-containing male cone associated with *Pseudofrenelopsis*. Ibid. **21**, 847–856.

ARCHANGELSKY, S. 1966. New Gymnosperms from the Tico Flora, Santa Cruz Province, Argentina. *Bull. Br. Mus. (nat. Hist.), Geol.* **13**, 261–295.

—— 1968. On the genus *Tomaxellia* (Coniferae) from the Lower Cretaceous of Patagonia (Argentina) and its male and female cones. *Bot. J. Linn. Soc.* **61**, 153–165.

BARNARD, P. D. W. 1968. A new species of *Masculostrobus* Seward producing *Classopollis* pollen from the Jurassic of Iran. Ibid. **61**, 167–176.

—— and MILLER, J. C. 1976. Flora of the Shemshak Formation (Elburz, Iran), Part 3: Middle Jurassic (Dogger) plants from Katumbagah, Vasek Gah and Iman Manak. *Palaeontographica*, (B), **155**, 31–177.

BATTEN, D. J. 1974. Wealden palaeoecology from the distribution of plant fossils. *Proc. Geol. Ass.* **85**, 433–458.

CHALONER, W. G. and LORCH, J. 1960. An opposite-leaved conifer from the Jurassic of Israel. *Palaeontology*, **2**, 236–242.

CHOW TSEYAN and TSAO CHENGYAO 1977. On eight new species of conifers from the Cretaceous of East China with reference to their taxonomic position and phylogenetic relationships. *Acta palaeont. sin.* **16** (2), 165–181. [In Chinese with English summary.]

COPE, M. J. and CHALONER, W. G. 1980. Fossil charcoal as evidence of past atmospheric composition. *Nature*, **283**, 647–649.

FONTAINE, W. M. 1889. The Potomac or younger Mesozoic flora. *Monogr. U.S. geol. Surv.* **15**, 1–377.

HARRIS, T. M. 1957. A Liasso-Rhaetic flora in South Wales. *Proc. R. Soc. B.* **147**, 289–308.

—— 1958. Forest fire in the Mesozoic. *J. Ecol.* **46**, 447–453.

—— 1979. The Yorkshire Jurassic Flora. V. *Coniferales*. British Museum (Natural History), London, 166 pp.

HIRMER, M. and HÖRHAMMER, L. 1934. Zur weiteren Kenntnis von *Cheirolepis* Schimper and *Hirmeriella* Hörhammer mit Bemerkungen über deren systematische Stellung. *Palaeontographica*, (B), **79**, 67–84.

HLUŠTÍK, A. and KONZALOVÁ, M. 1976. Polliniferous cones of *Frenelopsis alata* (K. Feistm.) Knobloch from the Cenomanian of Czechoslovakia. *Věst. ústřed. Úst. geol.* (Praha), **51**, 37–46.

HÖRHAMMER, L. 1933. Über die Coniferen-Gattungen *Cheirolepis* Schimper und *Hirmeriella* nov. gen. aus dem Rhaet-Lias von Franken. *Bibliotheca bot.* **27** (107), 1–34.

JUNG, W. 1968. *Hirmeriella münsteri* (Schenk) Jung nov. comb., eine bedeutsame Konifere des Mesozoikums. *Palaeontographica*, (B), **122**, 55–93.

KENDALL, M. W. 1947. On five species of *Brachyphyllum* from the Jurassic of Yorkshire and Wiltshire. *Ann. Mag. nat. Hist.* (11), **14**, 225–251.

—— 1949. On a new conifer from the Scottish Lias. Ibid. (12), **2**, 299–307.

LAUVERJAT, J. and PONS, D. 1978. Le gisement Senonien d'Esgueira (Portugal): Stratigraphie et flore fossile. *C. r. 103ᵉ Cong. Soc. sav.* (Nancy, 1978) *Sci.* **2**, 119–137.

MUIR, M. and VAN KONIJNENBURG-VAN CITTERT, J. H. A. 1970. A Rhaeto-Liassic flora from Airel, North France. *Palaeontology*, **13**, 433–442.

NATHORST, A. 1893. Pflanzenreste aus dem Noecom von Tlaxiaco. *In* FELIX, J. and LARK, H. (eds.). *Beiträge zur Geologie und Paläontologie der Republik Mexico*. Leipzig, Theil 2, Heft 1, 51–54.

PONS, D. 1979. Les organes reproducteurs de *Frenelopsis alata* (K. Feistm.) Knobloch, Cheirolepidiaceae du Cenomanien de l'Anjou, France. *C. r. 104ᵉ Congr. Soc. sav.* (Bordeaux, 1979) *Sci.* **1**, 209–231.

—— and BROUTON, J. 1978. Les organes reproducteurs de *Frenelopsis oligostoma* (Cretace, Portugal). Ibid. (Nancy, 1978) **2**, 139–159.

REYRE, Y. 1970. Stereoscan observation on the genus *Classopollis* Pflug 1953. *Palaeontology*, **13**, 302–322.

SCOTT, A. C. and COLLINSON, M. E. 1978. Organic sedimentary particles: results from scanning electron microscope studies of fragmentary plant material. *In* WHALLEY, W. B. (ed.). *Scanning electron microscopy in the study of sediments*. Geo. Abstracts. Norwich, England.

VAN KONIJNENBURG-VAN CITTERT, J. H. A. 1971. *In situ* gymnosperm pollen from the Middle Jurassic of Yorkshire. *Acta Bot. neerl.* **20**, 1–97.

—— 1972. Some additional notes on male Gymnosperm fructifications from the Jurassic flora of Yorkshire. Ibid. **21**, 95–98.

WATSON, J. 1977. Some lower Cretaceous conifers of the Cheirolepidiaceae from the U.S.A. and England. *Palaeontology*, **20**, 715–749.

ZHANG CHUNBIN 1962. Early Cretaceous sporo-pollen complex from Kiangsu. *Acta palaeont. sin.* **10** (2), 246–286. [In Chinese with Russian summary.]

ZHOU ZHIYAN and CAO ZHENGYAO 1979. Some Cretaceous conifers from Southern China and their stratigraphical significance. *In* Inst. Verteb. Palaeont. and Palaeoanthrop., and Inst. Geol. and Palaeont. (ed.). *Mesozoic and Cenozoic Red-beds of South China*. Sci. Press, Beijing, 218–222. [In Chinese.]

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